NOTES AND LITERATURE

HEREDITY

The Nature of "Unit" Characters.—One of the clearest presentations of Mendelian principles that has appeared recently is that of Dr. E. Baur in *Beihefte zur Medizinischen Klinik*, Vol. 4, 1908, pp. 266 et seq. He has given special attention to inheritance in crosses between the various varieties of *Antirrhinum majus*. He states that he knows 250 distinguishable varieties of this species, but he has never found amongst them characters that do not obey Mendel's law. He has demonstrated fifteen pairs of characters for the species, which is more than the number of chromosomes present, from which fact he concludes that the chromosome as a whole can not be considered as the basis of Mendelian unit characters. Others have cited as a basis for the same belief that more character pairs are known in Pisum than there are chromosomes present in the cells. This conclusion is not a necessary one, as is seen in the following. Speaking in a general way, the chromosomes are present in pairs of homologues. For each pair in the cells of a given individual there is a homologous pair in the cells of other individuals of the species. For convenience we may designate one of these pairs as A chromosomes, a second as B chromosomes, etc., the same pairs as a rule being found in different individuals of the same species.

If we consider the species as a whole, the number of pairs of A chromosomes is equal to the whole number of cells in all the individuals of the species. It is conceivable that, since certain of these A chromosomes may trace back thousands of generations before their ancestral lines unite, it is possible that there may be an indefinite number of subgroups of A chromosomes in the species, and that each subgroup may represent a heritable difference from other groups. But each of these subgroups would represent a Mendelian character. Hence, there might possibly be an indefinite number of Mendelian character pairs in a species having only a single pair of chromosomes.

But these characters could not all exist in one individual. Only two of the subgroups could be present together. Hence, in such a species, only two independent (not correlated) domi-

nant characters could be present, and these two would present a case of what Bateson calls spurious allelomorphism, for they would separate from each other in the reduction division.

It is clear, therefore, that the presence *in a species* of more Mendelian character pairs (presence and absence constituting a pair) than there are chromosomes does not prove that Mendelian characters do not appertain to the chromosome as a whole. If, however, in a species having one pair of chromosomes we could get *into a single individual* more independent character pairs than two, or if we can get even two dominant characters that are independent of each other, and not allelomorphic to each other, then we should have proven that Mendelian characters do not appertain to whole chromosomes. In general, if, in a species having 2n chromosomes, we can bring together in a single individual more than n independent dominant characters, no two of which are allelomorphic to each other, then it would be proved that Mendelian phenomena are not simply phenomena of the chromosomes. In a recent communication to the writer, Dr. Baur recognizes the justice of the above point of view and hopes to be able to test the matter in the near future. Dr. Shull will make a similar test at the Cold Spring Harbor Station. This, it would seem, is a simple and direct method of testing the validity of the theory advanced by many investigators, that the chromosome itself is the basis of the so-called unit character.

Even if this theory should be substantiated, it does not follow that the chromosome represents a unit character in the sense in which the term unit character is understood by most Mendelists. Shull has very justly pointed out[1] that "there is no evidence of the existence of a pair of internal units (allelomorphs)." The term "unit" has been applied to Mendelian characters on the assumption, which I regard as untenable, that there is in the germ plasm a definite organ set aside for each hereditary character. An elaborate theory of inheritance and evolution (De Vries) has been erected on this assumption. Mendelian phenomena can be explained in a wholly different manner, and one which is more consistent with the idea of the chemical basis of life processes, as the following illustration shows.

Let us designate the chromosome pairs in our common domesticated cattle as A, B, C, . . . L. Let us assume that the chromosomes in each of these pairs are capable of several types of metabolic activity, and that each of them, by its action on the nutritive materials furnished it, gives rise in the cell to as many

[1] See *Science*, February 12, 1909.

metabolic products as it has metabolic activities. Doubtless some of these products will be similar for a number of chromosomes. We may thus represent the chromosomes and their functions:

(AA) — functions	a,	b,	c,	d,		
(BB) — "		b,	c,	d,	e.	
(CC) — "	a,	b,		d.		
(EE) — "	a,	b,				f.
Etc.		Etc.				

Now, of the numerous B chromosomes in the species, some may perform the function e in a manner differing from the others. This function may fail entirely in some of them. Let us assume that the production of horny substance requires that the functions a, b, e and f shall be normal. If in a given group of individuals the function e fails, which function may represent the production of a given chemical substance in the cell, then horns fail to develop. Individuals without horns would thus be represented as follows:

(AA) —	a,	b,	c,	d.	
(BB) —		b,	c,	d.	
(CC) —	a,	b,		d.	
(EE) —	a,	b,			f.
Etc.		Etc.			

Omitting from consideration those chromosomes which are not concerned in the hereditary difference in question and remembering that the poll character is dominant, the heterozygote between the horned and polled forms would be

B — b, c, d, e; B — b, c, d (heterozygote polled).

Generation F_2 would consist of

1. B — b, c, d, e; B — b, c, d, e (horned).
2. B — b, c, d, e; B — b, c, d (heterozygote polled).
3. B — b, c, d; B — b, c, d (homozygote polled).

or three polled to one horned. Thus we derive the well-known Mendelian ratio entirely independently of any idea of unit character in the germ plasm. Rather we assume that horns are due to the presence in the cell of certain substances each produced by the chromosomes, as a result of their *chemical constitution;* and the poll character is due to the failure of a *single* chromosome to perform a particular function. When a hereditary difference between two varieties is thus due to a difference in a *single* set of homologous chromosomes, such difference will be-

have as a simple Mendelian character. If it be due to differences in two sets, it will behave as a compound character of two factors, and so on.

All known Mendelian phenomena may thus be explained as due to differences in the chemical constitution of the chromosomes in different groups. It is thus seen that Mendelian phenomena lend no support to the theory that each hereditary character is represented in the germ plasm by a separate entity.

The question as to the nature of the chromosome differences which are thus seen to be able to account for the phenomena first interpreted by Mendel will be considered at another time. The differences between the metabolic activities of homologous chromosomes here assumed may be due to differences in the relative amounts of given substances in the chromosomes concerned, or they may be due to differences existing in different *regions* of the chromosomes. In the present state of our knowledge of the chromosomes we are not ready for any theory on this point. Should Shull or Baur succeed in getting into a single individual more independent (neither correlated nor allelomorphic) dominant characters than there are chromosome pairs, then we shall at least know that the chromosome as an individual structure is not responsible for Mendelian characters. This is the one question which must be settled before Mendelian theory can make further progress.

Much recent work has been done which bears on the relation between chromosomes and hereditary characters.

First of these should be mentioned the important contribution made by Professor E. B. Wilson, published in *Science*, January 8, 1909. This paper is so accessible that it is unnecessary here to review it in full. Suffice it to say that Professor Wilson and his students have demonstrated an important relation between sex and certain chromosomes and chromosome groups. In general, the cells of the species studied contain an "X-element" which in some species consists of one chromosome, in others of two, in others three, and in one species of four chromosomes, but which acts as a unit in the reduction division; *i. e.*, all the chromosomes of the "element" pass to the same pole. In all the species studied, the cells of the female contain two of these X-elements, while those of the male contain but one. The males of some of the species contain no homolog (synaptic mate) for this element, but others contain an element which Wilson calls the Y-element, with which the X-element pairs in the reduction division. In every case the Y-element, when present, consists of a

single chromosome. In every case, therefore, the female is homozygote for the X-element, while the male is heterozygote either for X and Y, or for X and absence of X. Wilson shows that the above relations hold in a wide range of organisms, and suggests that it may be a very general relation. There are reasons however, for suspecting that the relation is not the same for all organisms. In a previous paper[2] I pointed out a number of cases which indicate that the female may be heterozygote and the male homozygote for sex, though some of the phenomena cited may be explained on a different basis. Miss Durham and Miss Marryatt[3] have recently worked out one of the cases referred to in my former article, which is a case in point. In certain strains of canaries, black-eyed females mated with red-eyed males give only black-eyed males and red-eyed females. This may be explained, as the authors point out, by assuming a correlation between eye color and sex. Letting X represent the chromosome element characteristic of the female and Y that of the male, assuming that Y is responsible for black pigment in the eye and that in some individuals Y has lost the pigment-producing power, the facts are rendered intelligible by the following assumptions regarding the gametic constitution of the types:

Black-eyed female = X Y–B, in which Y and B belong to the same chromosome element.

Red-eyed male = Y–b Y–b, where the function B is absent.

Here the females produce two kinds of eggs, namely, X and Y–B, while the males produce one kind of sperm (Y–b). This gives progeny of two types, namely, X Y–b (red-eyed females) and Y–B Y–b, black-eyed males. All the phenomena cited by Miss Durham and Miss Marryatt are explicable by assumptions similar to the above, though the occasional occurrence of black-eyed hens in the mating of black-eyed hens with pink-eyed cocks renders it necessary to assume that in some hens the X-element can also give rise to black pigment, or at least stimulate its production in some other element.[4] The facts cited in my previous paper regarding the inheritance of the bar character in the plumage of poultry further indicate that the female and not the male may be heterozygote for sex, as do also Doncaster's results

[2] AMERICAN NATURALIST, September, 1908.

[3] Rep. IV, Evol. Com., Roy. Soc.

[4] The gametic constitution here assumed is not that of the authors. They assume that *B* and *Y* are separate, but that *B* is "repelled" by *X*, thus giving the same results as above.

with the moth Abraxas. It is hoped Professor Wilson may be able to make cytological studies on some of these cases.

The fact that such characters as eye color in canaries, barring in poultry, and melanic types in Abraxas may be coupled with sex points strongly to the chromosomic nature of these characters. The work of Professor R. R. Gates, and that of Miss Annie E. Lutz on the chromosomes of Œnothera points strongly to the assumption that chromosomes are the elements with which we have to deal in the study of hereditary characters. Their results indicate that mutations of the De Vriesian type are due to accidents in mitosis. Miss Lutz remarks:[5]

> The numbers of chromosomes are closely associated with external characters in the first and last, and probably also in the second group.

Professor Gates has also expressed the opinion that abnormal chromosome behavior may account for the mutation phenomena observed by De Vries. It seems probable, therefore, that mutations of this character do not represent what we may call normal evolutionary changes, but that the latter must be sought in changes in the chemical constitution of the chromosomes.

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ENVIRONMENT

The Effect of Environment upon Animals.—"Katy-did, Katy-didn't" seems to continue to be a fair summary of the situation with respect to the heredity of acquired characters and the part played by environment in evolution. Wallace wrote in the *Fortnightly Review* (January, 1908) restating his belief in natural selection and recommending a careful study of Reid's "The Principles of Heredity" and Ball's "Are the Effects of Use and Disuse Inherited?" Rev. Henslow followed his advice and has published a short, suggestive and very readable book[1] on "The Heredity of Acquired Characters in Plants," in which he states with even more assurance than before the conclusion of his "Origin of Plant Structures," that "the Origin of Species is due to the joint action alone of the two great factors of evolution—*Variability* and *Environment*—without the aid of natural selection." This additional assurance seems to be the result of the growth of the ecological school of botanists and his belief that ecologists are "all at one" in accepting the fact that evolution in plants is the result of the effects of the environment which *can* become heredity.

[5] *Science*, February 12, 1909.

[1] London, John Murray, 1908, 107 pp.